

# A NEW PHILLIPSAEINID TETRACORAL FROM THE DEVONIAN OF NEW SOUTH WALES

by A. J. WRIGHT

**ABSTRACT.** *Fromeophyllum climax* gen. et sp. nov. is a phillipsaeinid tetracoral from the Mount Frome Limestone near Mudgee, New South Wales, Australia, where it occurs over a stratigraphical thickness of 98 m, ranging between Dalejan (Early Devonian) and possibly Eifelian (Middle Devonian) strata. The subfamily assignment is based on a close similarity to *Macgeea touti* Pedder, which appears to be ancestral to *F. climax*.

Silicified specimens show *F. climax* to be a polymorphic fasciculate form which undergoes up to three phases of parricidal peripheral increase. When basal structures are preserved, *F. climax* is mostly found attached to various types of fossil skeletons which offered a firm substrate above the muddy sea floor by sheaths of skeletal material. Calcareous specimens show a well-defined vertical series of horseshoe dissepiments outside which are horizontally disposed ranks which consist alternately of mostly horseshoe dissepiments and flat dissepiments. Outside this zone normal dissepiments are developed which are proximally and outwardly inclined. This outermost array of skeletal material often spreads down the side of the colony over the wall of the trunk, demonstrating the presence of a highly extensile edge zone and everted calyx. Polymorphism is manifest in the diameter and number of septa developed in each of the several generations within a colony.

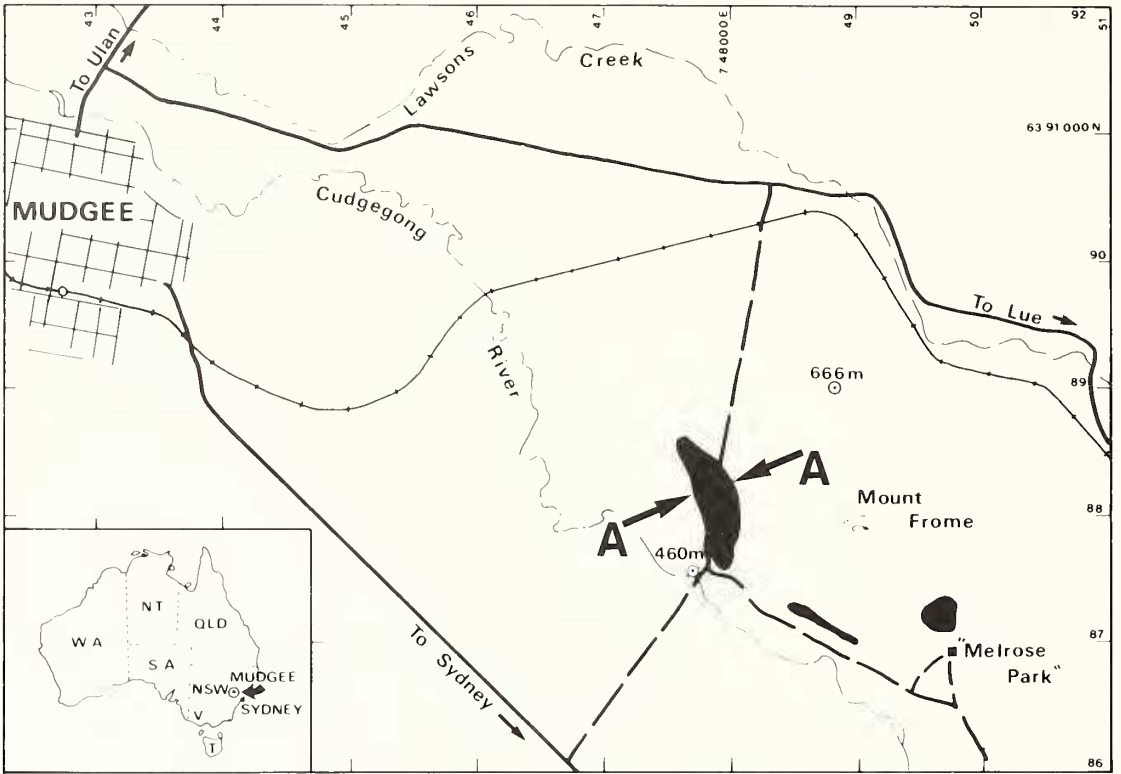
ON the western and southern flanks of Mount Frome (650 m) which is located 13 km east of Mudgee, New South Wales, Australia (text-fig. 1), the Mount Frome Limestone (Wright 1966) is well exposed. Despite the early discovery and recognition of this limestone and others in the area (Stutchbury 1852; Taylor 1879; Clarke 1978), little attention was paid to its rich faunas until the work of Game (1935). Game (1935, p. 209) preferred a Silurian age, in contrast to the Devonian age inferred by Clarke (1878, p. 16).

## BIOSTRATIGRAPHY AND AGE

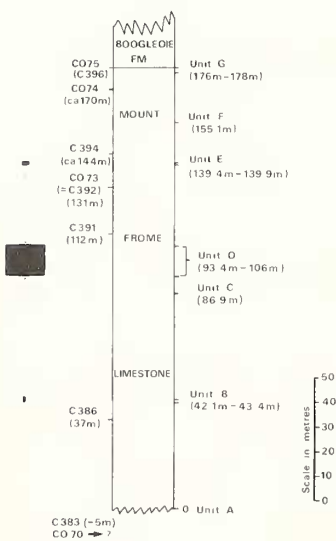
The Mount Frome Limestone is exposed along strike for some 5 km (text-fig. 1) and contains (especially in the northern outcrops) a number of units which have been characterized by their faunas (Wright 1969). These units are separated by poorly exposed or poorly fossiliferous intervals and are recognizable along strike over various distances. For example, although *F. climax* and other characteristic faunal elements persist to outcrops at 'Melrose Park' in the south (text-fig. 1), no sequence of units has been recognized there; further, faunal elements such as *Melrosia* occur only in these southernmost outcrops (Wright 1966). The total thickness of the Limestone recognized in the most northerly outcrops is 178.5 m (text-fig. 2), *F. climax* being known from 42.1 to 140.0 m (Unit B to Unit E inclusive). In Units B and D, *F. climax* occurs with two-hole crinoid debris (Johnson and Lanc 1969).

Various Devonian ages have been suggested for the Mount Frome Limestone. Wright (1965, 1966, 1967, in Packham 1969) favoured a Middle Devonian age for the entire formation on the basis of tetracoral and brachiopod ranges as then understood in Eastern Australia. Conodont data subsequently permitted Philip (1974) and Pickett (1978) to suggest a Middle Devonian (Eifelian) age for the uppermost 50 m of the Limestone, the entire underlying sequence being considered Early Devonian.

According to Pickett (1978, p. 98) the Mount Frome conodont '... faunas represent the units of *Polygnathus perbonus perbonus*, *P. perbonus* n. subsp. D, and *P. costatus costatus*' of Perry, Klapper and Lenz (1974). Following nomenclatural changes these units could be transformed into the *inversus*



TEXT-FIG. 1. Locality map showing *Fromeophyllum*-bearing outcrops of Mount Frome Limestone. Grid lines (at 1000 m intervals) and topographic data are from the Mudgee 100000 topographic sheet (1st edn., sheet 8832). Approximate location of section A-A arrowed.



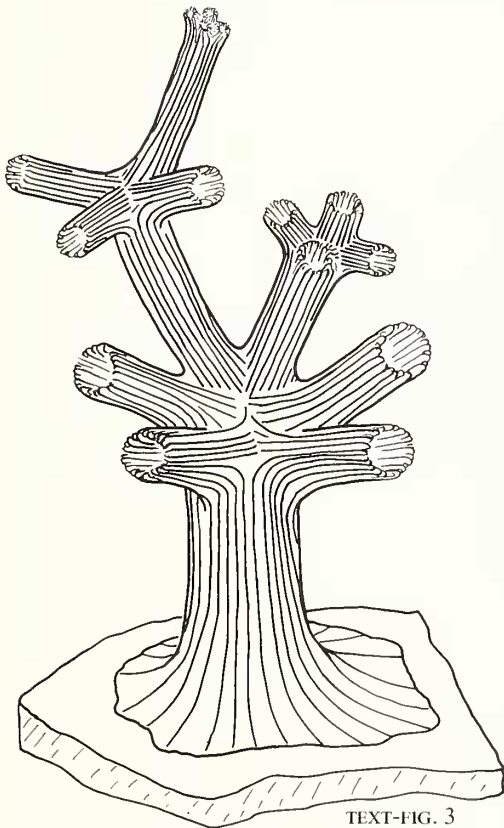
TEXT-FIG. 2. Measured section through Mount Frome Limestone showing positions of units based on macrofossils. *F. climax* ranges from Unit B to Unit E inclusive. The section was measured near the northern end of the northern outcrop area (see text-fig. 1). Unit A lies about 10 m stratigraphically above the basal beds exposed in an anticline. Because of this anticline, Pickett's (1978) section appears some 60 m too thick. The positions in my measured section, of Pickett's (1978) localities—shown as numbers on the left side of the column—are reasonably accurate. On the basis of Pickett's results (1978, fig. 2) *Polygnathus serotinus* appears at 112 m. Whereas my results show that this species is present in Unit A.

Zone; the *serotinus* Zone; and the *patulus* Zone respectively (Klapper and Ziegler 1979). Of these, only the latter is considered Eifelian, and then only in part (Weddige and Ziegler 1977). Correlation of these conodont Zones with the European stages (Chlupáč 1976) would tentatively indicate that the Mount Frome Limestone was equivalent to at least parts of the Zlichovian, Dalejan, and Eifelian stages (cf. Jackson, Lenz and Pedder 1978, fig. 6). Conodonts including *Polygnathus serotinus* have recently been recovered from Unit A by the author, indicating that this Unit is no older than Dalejan (Klapper and Ziegler 1979). Equally, an Eifelian age for part of the Mount Frome Limestone rests on Philip's (1974) report of *P. costatus patulus* at Mount Frome itself.

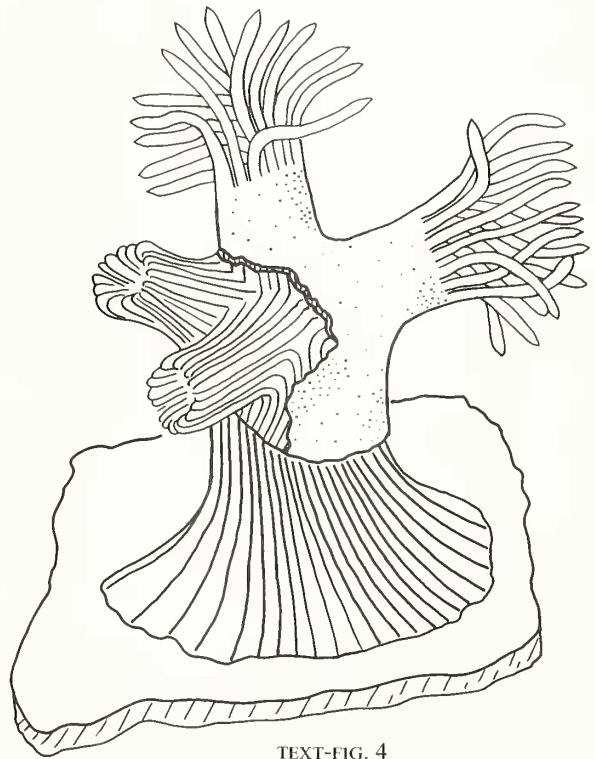
#### TERMINOLOGY

In general, the morphological terms used here are those of Moore, Hill and Wells (1956, p. F245). However, a few aspects of *Fromephyllum* are discussed in detail below.

1. A colony of *F. climax* may undergo peripheral (Fedorowski and Jull 1976) parricidal increase several times (text-fig. 3), producing offsets of the resultant generations which differ from each other and from the 'parent' (see below). These episodes of increase are here referred to as *phases* and the



TEXT-FIG. 3



TEXT-FIG. 4

TEXT-FIG. 3. Reconstruction of a colony of *F. climax* showing three phases of increase. Epitheca, intraseptal grooves, competitors for space on substrate, and encrusting organisms omitted. About  $\times 1$ .

TEXT-FIG. 4. Reconstruction of a colony of *F. climax* showing one phase of increase, with only four offsets produced rather than the normal six. Soft parts of two polyps are shown (tentacles especially idealized), with the edge zone extending down the wall of the trunk and removed to show 'overflow' skeletal material in which septal structures are not concordant with those of trunk. It is not certain that the soft parts were continuous between offsets, as their length increased to maturity. About  $\times 2$ .

offsets produced thereby are termed *first-order offsets*, *second-order offsets*, and *third-order offsets*. As some offsets gave rise to their own offsets, the term parent loses its generally accepted meaning and the initial segment of the colony (prior to the first phase of increase) is termed the *trunk*. Offsets may thus be loosely termed *branches*.

2. The above terminology must be compared with that of Fedorowski (1978). *F. climax* could be described as a quasi-colony (Fagerstrom and Eisele 1966), wherein only one mature corallite—the large basal portion—is recognised. Fedorowski (1978, p. 206), however, regarded the ability to produce offsets as one of the best criteria of maturity, so on that basis the first- and second-order offsets in *F. climax* should be considered mature. The persistent polymorphism of *F. climax* from various horizons and lithologies suggests genetic control of the polymorphism, rather than control by environmental factors producing progressively more diminutive offsets. Further, the varied and abundant associated fauna includes a number of large-shelled species which certainly would not indicate a deficient environment. Composite colonies, as described by Fedorowski (1978), are represented by a few specimens of *F. climax* (Pl. 93, figs. 7, 18*b*). These are regarded as contemporaneous colonies formed by larvae settling at the same time and in sufficiently close proximity to ensure physical contact between the colonies. These sometimes produce corallites resembling lost structures (Fagerstrom and Eisele 1966).

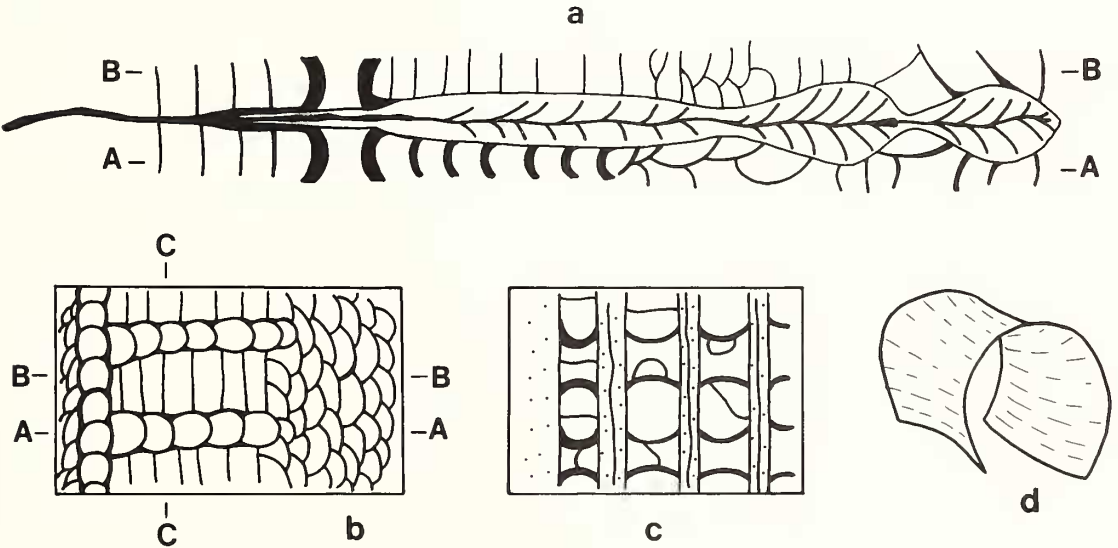
The species is termed polymorphic, a description which it merits in two ways. Firstly, equivalent growth stages of different colonies may be morphologically distinct. Secondly, the various orders of offsets within a colony (text-fig. 3) are usually quite different in diameter and number of septa. This notion of polymorphism in *F. climax* warrants inclusion of all silicified specimens in the one species (see section on variation below).

3. Since the introduction of the term 'horseshoe dissepiments' (Lang and Smith 1935), their morphology has been poorly appreciated until recently. The original authors were, with many others, concerned only with their presence or absence in thin sections. As these dissepiments appear to have considerable importance in tracing phylogenies, a clear understanding of their three-dimensional geometry is essential to distinguish them from different dissepiments. Many authors have commented on the characteristic shape and vertical continuity of the horseshoe series, which Pedder (1966, p. 187) described as a 'collar'. Fenton and Fenton (1924, pp. 48–49) referred to these horseshoes on the colony surface as the pseudothecial ring. Scrutton (1968, p. 261) noted the '... distinctive double wall ...' in transverse sections of tetracorals containing horseshoes. Sorauf (1978, p. 819) drew attention to the ease of identification of '... the row of horseshoe dissepiments by their thickness ...' and termed this feature visible in transverse section a 'napkin ring'. Associated with the horseshoes, as many authors have remarked, is the spindle-wise dilation of the septa. Certainly, spindle-wise dilated septa located on this *double* ring are seen in transverse sections of species possessing horseshoe dissepiments, and are among the characteristic morphological features of the subfamily. But equally important are the mutually convex intercepts produced by a transverse section through a single horseshoe dissepiment. This has been realized previously by Schouppé and Stacul (1963, figs. 10–14), Scrutton (1968, p. 261), and Brice and Rohart (1974, fig. 2*a*); the latter authors' diagram clearly shows the form which an individual horseshoe must have to produce the characteristic intercepts in transverse sections. The depressed or sagging nature of the dissepiment ('saddle-shaped'—Scrutton 1968) is shown here diagrammatically (text-fig. 5*d*).

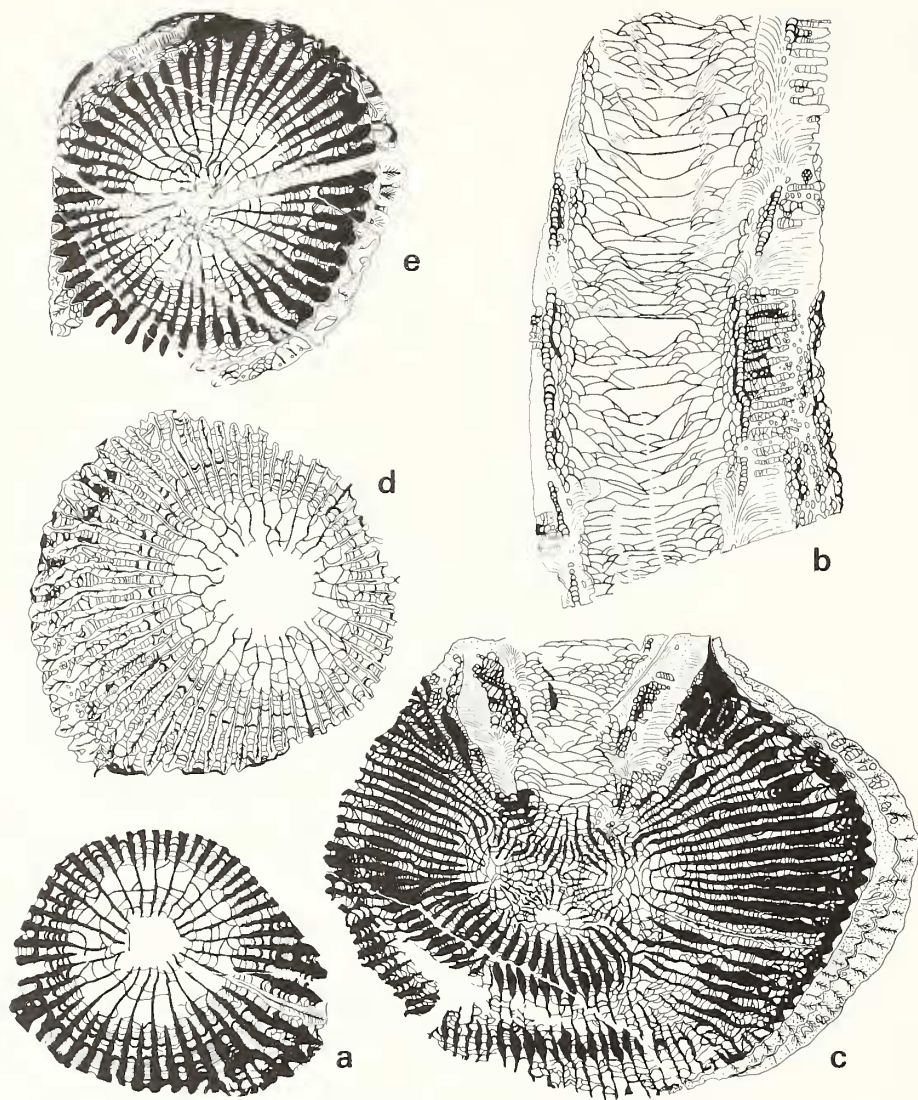
Tetracorals with horseshoe dissepiments normally display, when the calyx is free from enclosing sediment, a raised rim to the tabularium (corresponding to the location of the horseshoes). Further, in solitary or fasciculate forms the epitheca may not extend to the rim of the calyx. This couplet of morphological features is loosely referred to as *exsert*, in connection with septa (Smith 1945, p. 27), corallites and 'cell walls' (Fenton and Fenton 1924, p. 46 *et seq.*), or calices (Wells 1956, p. F421; Sorauf 1978, p. 823). As the word *exsert* indicates a projection or protrusion, it should be restricted to the septa where they project distally above the horseshoes. No term is needed to denote the condition in which epitheca is lacking distally, as in *Macgeea* (e.g. Smith 1945, pl. 24). However, the widely flaring calyx can be referred to as *everted* (e.g. Pickett 1967, p. 12), describing the way in which the peripheral area is turned outwards.

Closely associated with the development of vertically disposed horseshoes is the development of divergent arrays of primary and secondary trabeculae, similar to those described by Jell (1969) as rhipidacanthine. The preservation of growth lines in the septa of available *F. climax* specimens is not good, but primary and secondary trabeculae can be clearly seen, especially in longitudinal sections in the median plane of a septum. The location of maximum development of secondary trabeculae in *F. climax* (text-fig. 5a) is outside the vertical horseshoes, quite different from that shown by Brice and Rohart (1974, fig. 4) for *Macgeea gallica gigantea*, and obviously related to the unique dissepimentarium (text-fig. 5b).

4. A striking morphological characteristic of *F. climax*, seen in both thin sections and silicified specimens, appears to result from an edge zone. This is the development of globose dissepiments outside the main dissepimentarium, outwardly and proximally inclined, and deposited on an epitheca, which is lacking from the underlying dissepiments. A number of phases of deposition of these dissepiments can sometimes be seen, especially in longitudinal section (text-fig. 7a) where in some cases the purpose (or at least the result) has been to extend greatly the area of basal attachment. In silicified and some calcareous material these phases can be seen to have produced sheets of skeletal material—septal in external appearance rather than dissepimental—which bear septa which are usually confluent with those on proximal parts of the trunk but occasionally (text-fig. 4) discordant. These sheets are mostly evident when they emanate from offsets and extend down the parent. Many specimens, however, suggest that this process was affecting the trunk and enlarging the basal attachment area (Pl. 93, figs. 3, 4, 5) prior to, as well as after, offset. Rózkowska (1953, figs. 18, 19) showed concentric deposits in transverse views of *Pexiphyllum ultimum* Walther; these are rather similar to the material in *F. climax*, but are caused by development of talons in only early ontogenetic stages.



TEXT-FIG. 5. Aspects of *F. climax*. a, transverse section through a major septum flanked by horizontal series of vertical flat plates lateral to horseshoes (at top) and horizontal series of horseshoes lateral to vertical series of horseshoes (at bottom). This view also shows dilation [presumably due to lamellar schlerenchyme (not seen, nor shown here)] associated with rhipidacanthine trabeculae as shown, and normal globose dissepiments lateral to horizontal series. The section lines A-A and B-B correspond to section positions in text-figure 5b. b, portion of longitudinal section (omitting septal dilation) showing dissepimental structure. Tangential section along C-C show in text-fig. 5c. c, simplified, diagrammatic tangential section along C-C of text-fig. 5 showing three interseptal spaces. Mutually convex dissepimental intercepts are the (horizontal) horseshoes; intervening dissepiments mostly vertical plates. See text-fig. 10c. d, idealized horseshoe dissepiment, emphasizing warped nature.



TEXT-FIG. 6. Drawings of *Fromeophyllum climax*. *a*, transverse and *b*, longitudinal views of holotype USGD 21248. *c*, paratype USGD 88213, transverse view showing offsets. *d*, paratype USGD 21177, transverse view. *e*, paratype USGD 21261, transverse view. All  $\times 3$ .

Wells (1957, p. 773) has considered that the development of an edge zone was one of the great advances made by post-Palaeozoic corals. If an edge zone is defined as extending downwards to the level of the original base and expanding over the substrate to give a broad base, then *F. climax* certainly possessed a structure capable of this but which, surprisingly, was of no obvious success in subsequent evolutionary pathways.

In some cases the edge zone did not extend right down to the substrate, as evidenced by the limits of the 'overflow' skeletal material, especially that from offsets. The absence of epitheca on many branches suggests that the offsets were connected by coenosarc. However, in both the above situations the epitheca may have been removed. Although the typical spoke-like appearance in

transverse view (Pl. 92, fig. 1) is due to removal of some outer parts of the skeleton, the evidence for epitheca in the few favourably preserved specimens is mostly weak or lacking except where developed beneath the edge zone skeletal deposits (but see text-fig. 8c).

The typical transverse view shows outer septal ends rather resembling spokes (Pl. 92, fig. 1); these are very similar to the costae shown for hexacorals by Wells (1956, fig. 243A). In many specimens there has been abrasion to different positions in the transverse sense, extending in some cases as far in as the horseshoes (Pl. 92, fig. 5). In other specimens, skeletal material deposited by the edge zone has been deposited unevenly around the parent (text-figs. 6c, d) and is deposited over skeleton which appears abraded in some examples and unabraded in others. Some skeletal material may even have been deciduous. But whatever process operated, the incomplete septa generally terminate at their thinnest point outside the zone of maximum dilation and it seems that the very common occurrence of this mode of preservation of 'septal spokes' indicates a section through an everted calyx lacking not only epitheca but also adventitious edge zone skeletal deposits (i.e. near the calical rim in a specimen as shown in Plate 93, fig. 10).

*Repositories.* Some material is deposited in the Department of Geology and Geophysics, University of Sydney (USGD) and some in the Australian Museum (AMF).

#### SYSTEMATIC DESCRIPTION

Phylum COELENTERATA

Class ANTHOZOA

Order TETRACORALLIA

Family PHILLIPSASTRAEIDAE Roemer, 1883

Subfamily PHILLIPSASTRAEINAE Roemer, 1883

Genus FROMEOPHYLLUM nov.

*Type Species.* *F. climax* gen. et sp. nov.

*Diagnosis.* Fasciculate Phillipsastraeinae characterized by a complex dissepimentarium in which there are two main zones of dissepiments outside the vertical series of horseshoes. There are firstly horizontal rows of vertical plates, these rows alternating with horizontal rows of horizontally disposed horseshoes. Outside these rows there may be a zone, deposited by an edge zone, of outwardly, proximally, and steeply inclined globose dissepiments, rarely enclosed by epitheca. Colonies show up to three phases of parricidal peripheral increase, producing up to six offsets in each phase. Colonies are polymorphic, as offsets of each phase of increase generally have progressively smaller diameter and fewer septa.

*Discussion.* Only one described species, *Macgeea touti* Pedder, 1966, has an outer dissepimentarium (text-fig. 10d) similar to that of *F. climax* and may belong to *Fromeophyllum*. If so, the generic diagnosis may have to be modified, as *M. touti* was considered solitary by Pedder (1966). Another form which may belong to *Fromeophyllum* is *Macgeea* sp. of Fontaine (1961, p. 103, pl. 20, figs. 1-2), but more information concerning the dissepimentarium is needed before a decision can be made. Tsien (1968, p. 450) introduced, apparently as a *nomen nudum*, the new genus *Senceliastraea* for fasciculate members of the Macgecinae. Presumably its dissepimentarium is much less complex than that of *Fromeophyllum*.

*Etymology.* The genus is named after Mount Frome, which in turn was named after Tom Frome, one of the early settlers in the area in the 1820s.

*Distribution.* The genus is known from Mount Frome, and possibly from New England (New South Wales) if *M. touti* belongs in *Fromeophyllum*. It is known from the Early Devonian, and ranges up into strata at Mount Frome which may be Middle Devonian.

*Fromeophyllum climax* sp. nov.

Plate 91, figs. 1–6; Plate 92, figs. 1–7; Plate 93, figs. 1–19; text-figs. 3–10

1979 *F. climax* Wright; in Packham (ed.), p. 132 (*nomen nudum*).

*Type Material.* Holotype USGD 21248 (TS, W53; LS, W52). Paratypes: USGD 21175 (W279, W280, both TS); USGD 21176 (TS, W605; LS, W606); USGD 21177 (W594, W595, both TS); USGD 21178 (LS, W1152); USGD 21251 (TS, W276; LS, W277); USGD 21254 (W1050, W1051, both TS); USGD 21261 (TS, W45); USGD 21262 (TS, W43); USGD 21266 (LS, W601); USGD 21267 (W1054, TS and LS); USGD 21268 (LS, W1055); USGD 21272 (LS, W1157); USGD 21273 (LS, W590); USGD 21274 (LS, W689); USGD 85221–35; USGD 88213–15; USGD 88217; USGD 88220; AMF 60656–65.

*Type Locality and Stratum.* All *F. climax* specimens are from the Mount Frome Limestone, near Mudgee, New South Wales. The species ranges through 97.8 m, from the base of Unit B to the top of Unit E (text-fig. 2). The holotype is from Unit D (94.4–108.4 m), locality Mu/iv/50. Other members of the type series arranged by horizon and locality are: Mu/iv/48—USGD 21175–6, 85233. (Unit B, north outcrop.) Mu/iv/50—USGD 21177–8, 21251, 21254, 21261–2, 85232, 85234, 88213, 88220. (Unit D, north outcrop.) Mu/iv/58—USGD 21266–8, 21270, 21272–4. (Unit D, middle outcrop.) Mu/iv/52—USGD 85221–31, 85235, 88214–15, 88217; AMF 60656–65. (Unit E, north outcrop.)

*Diagnosis.* *Fromeophyllum* in which the tabularium reaches up to 11 mm in diameter and there are up to 38 (usually 25 to 30)  $\times$  2, septa.

*Description.* Fasciculate colonies, with branches diverging strongly (at least initially); largest colony about 100 mm in maximum dimension. Non-silicified specimens appear more gregarious than silicified specimens. Trunk of colony up to about 50 mm in length before branching, and generally less than 20 mm in diameter. Some trunks can be seen from interseptal grooves to have undergone a form of 'twisting' (Pl. 93, fig. 3; text-fig. 4). Other colonies give an impression of asymmetry in that some daughters bud whereas others do not. Many colonies undoubtedly composite.

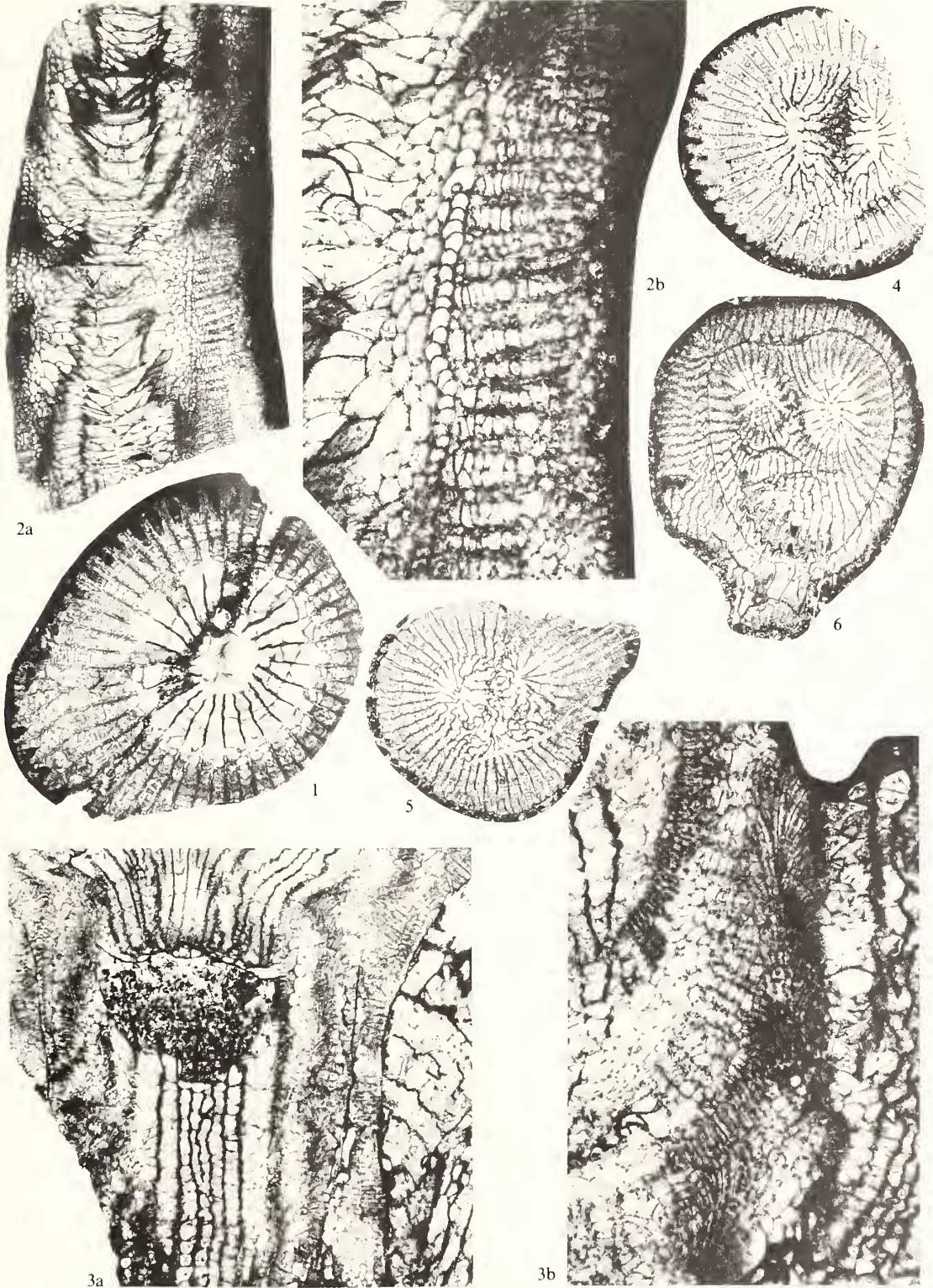
Basal attachment area (Pl. 93, figs. 4, 5) often greater than 30 mm in diameter, and may be greatly and asymmetrically extended; angle at which base meets substrate varies greatly. Many colonies incorporate, near base, corals or other skeletal material; it is not clear whether these were symbiotic or overgrown by *F. climax*. Apparently juvenile *F. climax*, on settling on a suitable substrate, rapidly increased diameter of attachment area while maintaining trunk height of about 10–15 mm. Rarely, flattish base is stripped of substrate and bears concentric zones of septal dilation, but no striking pattern of septal insertion observed.

Increase almost invariably parricidal, rarely lateral. First phase of parricidal increase usually produces three to six offsets (Pl. 93, figs. 1, 8, 17, 19) arranged more or less radially around a shallow, wide area (text-fig. 3); rarely two offsets. Initially tiny divergent first-order offsets (Pl. 93, figs. 18, 19) rapidly separate and reach length of up to 50 mm and diameter of about 15 mm before increase (text-fig. 3). Second-order offsets may branch at length of 20 mm. Second and third phases of increase produce three or four offsets, with failure of offsets

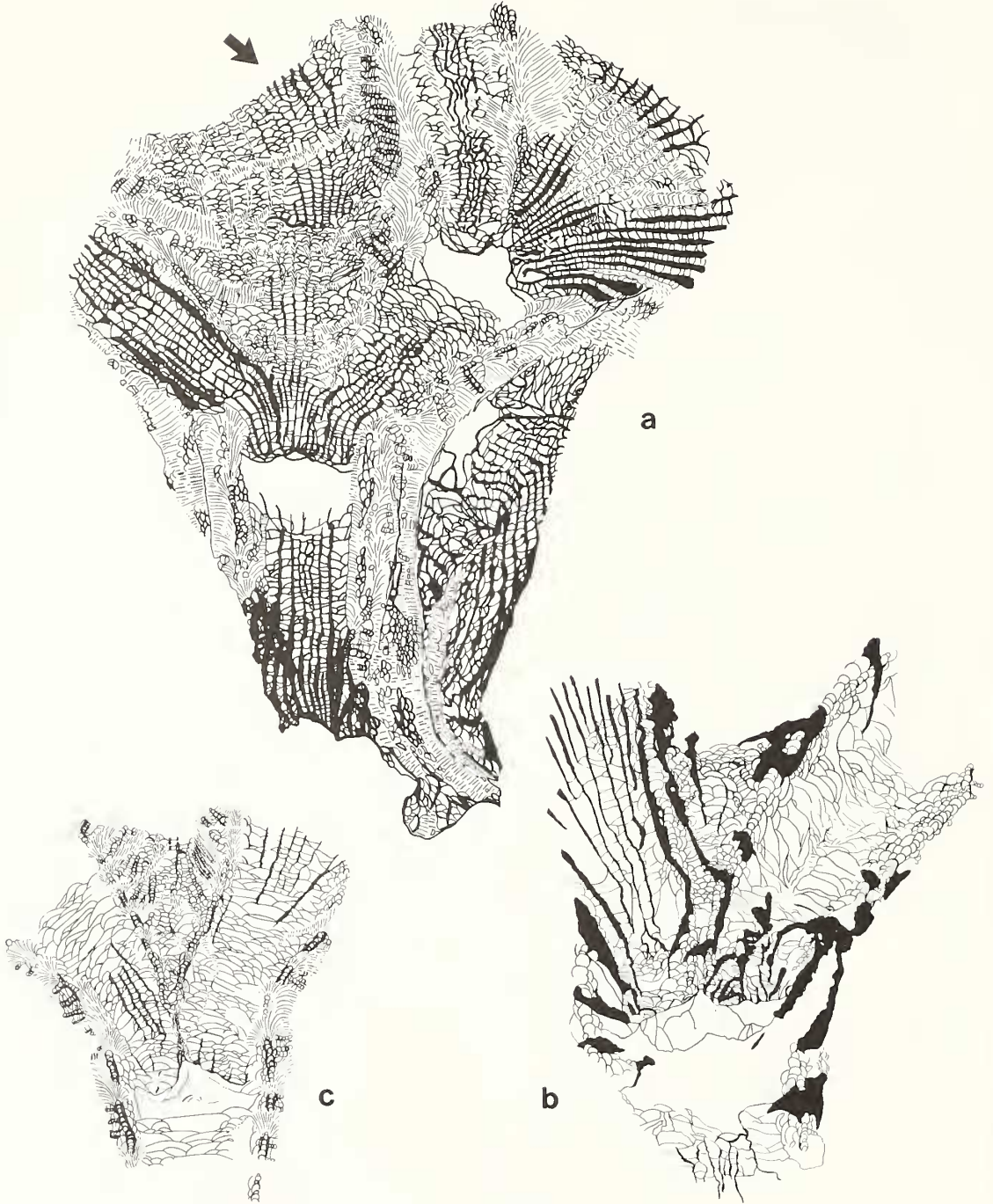
## EXPLANATION OF PLATE 91

Figs. 1–6. *Fromeophyllum climax* gen. et sp. nov. All from Unit D, Mount Frome Limestone, near Mudgee, New South Wales. Early–Middle Devonian. 1–2, holotype USGD 21248, 1, transverse  $\times$  4. 2a, longitudinal,  $\times$  3. 2b, enlargement of portion of previous figure, clearly showing dissepimental structure,  $\times$  9. 3a, 3b, paratype USGD 21266 (see text-fig. 7a), 3a, longitudinal of trunk region showing cavity formed by first phase of increase but more importantly, on both sides of trunk, overgrowth by edge zone deposits,  $\times$  6. 3b, longitudinal of part of second-order offset (see region of text-fig. 7a indicated by arrow) clearly showing dissepiments and trabeculae,  $\times$  8. 4, paratype USGD 21254a, transverse showing two juvenile offsets,  $\times$  3. 5, paratype USGD 21262, transverse showing three juvenile offsets,  $\times$  3. 6, paratype USGD 21251, transverse showing two successful offsets and one apparently aborted offset; cordate line separates offsets (inside) from edge zone deposits (outside),  $\times$  2.





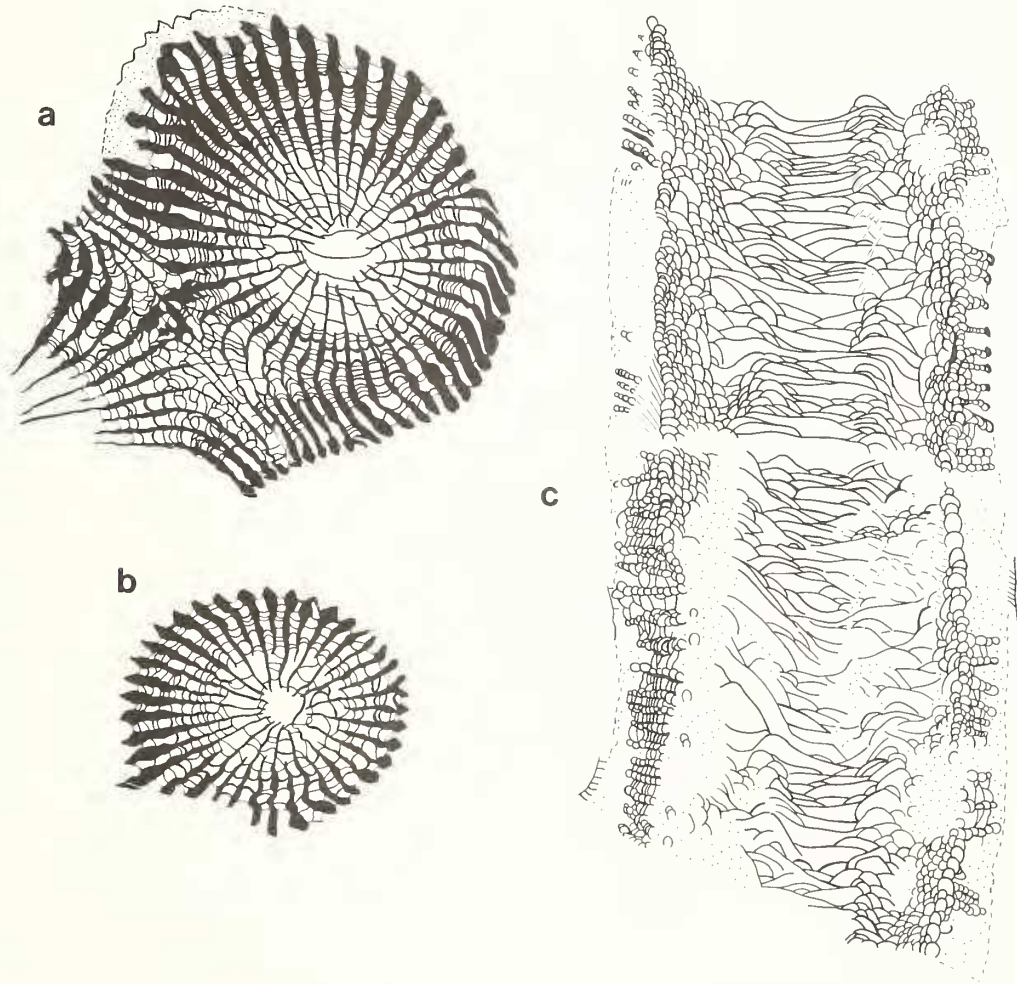
WRIGHT, *Fromeophyllum*



TEXT-FIG. 7. Drawings of *Fromeophyllum climax*. *a*, paratype USGD 21266, longitudinal view showing overgrowth of trunk by skeletal deposits of offsets and trunk. Arrow indicates approximate area shown in Plate 91, fig. 3*b*. *b*, paratype USGD 21272, longitudinal view showing increase. *c*, paratype USGD 21268, longitudinal view showing increase. All  $\times 3$ .

common in third-phase of increase, which is the least abundant. Third-order offsets (Pl. 93, fig. 2) always very short (less than 10 mm), and easily recognizable where second-order branch preserved, but also strongly resemble tiny (diameter about 5 mm) specimens (Pl. 93, figs. 18, 19) which are epifaunal in the encrusting manner normal for *Fromeophyllum*. Tiny epifaunal specimens may be sexually produced individuals, and are presumably failed normal *F. climax* protocorallites.

Calices generally everted (although not clearly so as in the case of *Macgeea*—see e.g. Rózkowska 1956, fig. 11*b*), flat-bottomed, and cylindrical. On outer walls of some individuals, former position of rim of 'overflowing' edge zone is marked by vestiges of epitheca and rarely by septa (of an offset) discordant with those of parent (see Pl. 93, fig. 3; text-fig. 4 for diagrammatic reconstruction). Concordant major and minor septa between offsets and parents are the general rule on outer regions of colonies. On distal surface of colony showing first-order offsets, septa of contiguous offsets generally abut sharply. Epitheca rare and must have been quite thin; it is often seen associated with offsets, especially second- or third-order offsets. Interseptal and intra-septal grooves developed where epitheca absent. Apparently fossulae of trunks continue through to offsets; external signs of (?) renewed septal insertion begin below first signs of offset but apparently correspond to level where septa of parent



TEXT-FIG. 8. Drawings of *Fromeophyllum climax* from Unit E (Mu/iv/52), northern outcrop area. All paratype USGD 85235. Trabecular structure poorly preserved. *a*, transverse view, juvenile specimen; *b*, transverse view, mature specimen; *c*, longitudinal view. All  $\times 3$ .

commence to withdraw from axis. In thin sections, and rarely in broken silicified branching trunks, offsets are floored collectively by a transverse surface (text-figs. 7a-c). Extreme diameter of many trunks may be due to 'overflow' of edge zone down to original substrate—that is, increase of trunk diameter by either offset tissue or trunk tissue.

In thin section, transverse views highly variable (Pl. 92, figs. 1, 2, 5; text-fig. 6a, c, d, e). This results from polymorphism (see above), and variable development of outer dissepimentarium which depends on extent of edge zone tissue. General nature of septa is as follows. Major septa are long, and equally but slightly withdrawn from axis; minor septa up to three-quarters of length of major septa. Septa generally straight, may be irregular, but are never carinate. Both orders only slightly dilated in tabularium, where they consist largely of thin dark lines forming axes of septa in inner part of dissepimentarium. Both orders of septa moderately dilated over horseshoes (text-fig. 5a), where trabecular structure is poorly defined but seems to consist of a few transverse blebs of trabeculae projecting into stereome. Outside this zone long rhipidacanthine trabeculae diverging from an irregular, wavy, central axis become easily discernible in a highly dilated zone, reaching up to 4 mm out from the vertical series of horseshoes. This is the prominent spindle in *F. climax*, extending well beyond zone of vertical plates (as seen in longitudinal sections) into zone of normal dissepiments, where thickening diminishes. Outside this main thickened zone several more zones of thinning and thickening may occur in the zone of normal globose dissepiments (text-fig. 5a). Trabeculae coarse and in a radial vertical plane diverge through at least 180° (Pl. 91, figs. 2b, 3a, 3b; Pl. 92, figs. 4, 7).

Epitheca mostly seen in thin section with certainty beneath (on axial side of) overgrowths deposited over pre-existing skeletal material. Discontinuities resulting from cessations in septal secretion occur in many specimens, again demonstrating periodic and often asymmetrical 'overflow'. One trunk specimen (text-fig. 8c), although poorly preserved, seems to possess epitheca in one region, flanking outwardly and downwardly inclined dissepiments. Silicified specimens, generally second-order offsets, may bear bands of epitheca.

Up to 38 (generally 25 to 30)  $\times$  2 septa are characteristic of trunk specimens, usually 12  $\times$  15 mm in diameter. Normally first-order offsets have up to 25  $\times$  2 (rarely 29  $\times$  2) septa, second-order offsets up to 23  $\times$  2 septa. These septal criteria depend on maturity of offset, as do tabularium diameter and corallite diameter.

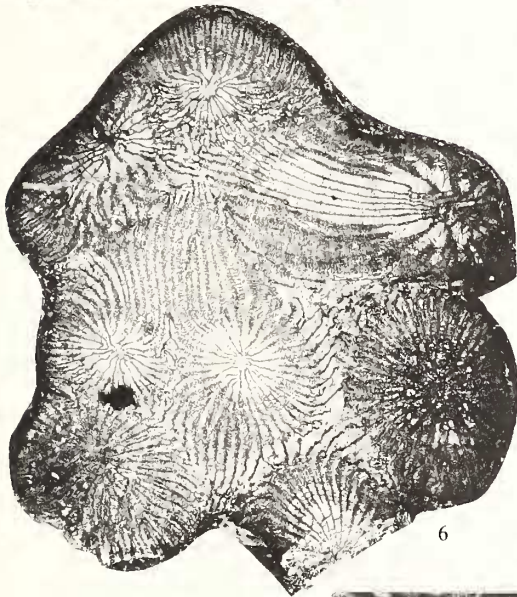
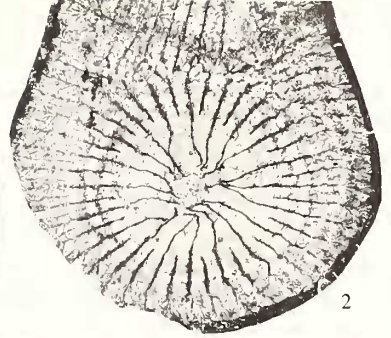
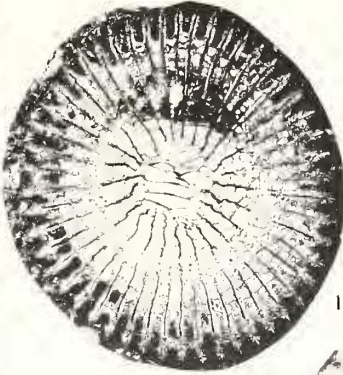
Tabularium diameter expands rapidly distally up to 11 mm, whereas corallite diameter depends on amount of overgrowth. In general, tabularium diameter of trunks is 9.0 to 11.5 mm, first-order offsets 6 to 9 mm and other offsets about 6 mm. Tabulae mostly complete and close-set, and may be flat, sagging, or domed; when incomplete consist of numerous small convex plates supplemented by small globose plates which occasionally form a periaxial elevation to the concave tabular floors. Calyx with wide floor which commonly has a flat-topped boss, steep walls, and apparently flat rims. Width of the tabularium variable, generally more than half corallite diameter. Many longitudinal sections exhibit apparently abortive phases of increase, as evidence by irregular tabular structures and spacing, with subsequent development of a wide, prominent tabula (Pl. 91, fig. 2a; text-fig. 9b).

Calical sections (text-figs. 10a, 10b) show that the distal few horizontal zones of horseshoe dissepiments outside the vertical horseshoe series are shorter (radially) than 'normal', the topmost zone being shortest, the next one longer, and so on until a normal length is attained. This strongly suggests an everted calyx with an 'overflow' of edge zone (see text-fig. 4 for diagrammatic reconstruction). There is no indication that each horizontal series of horseshoes represents an abrupt lateral deflection of the vertical horseshoe series, although there may be a slight curvature in horizontal series at junction with vertical series.

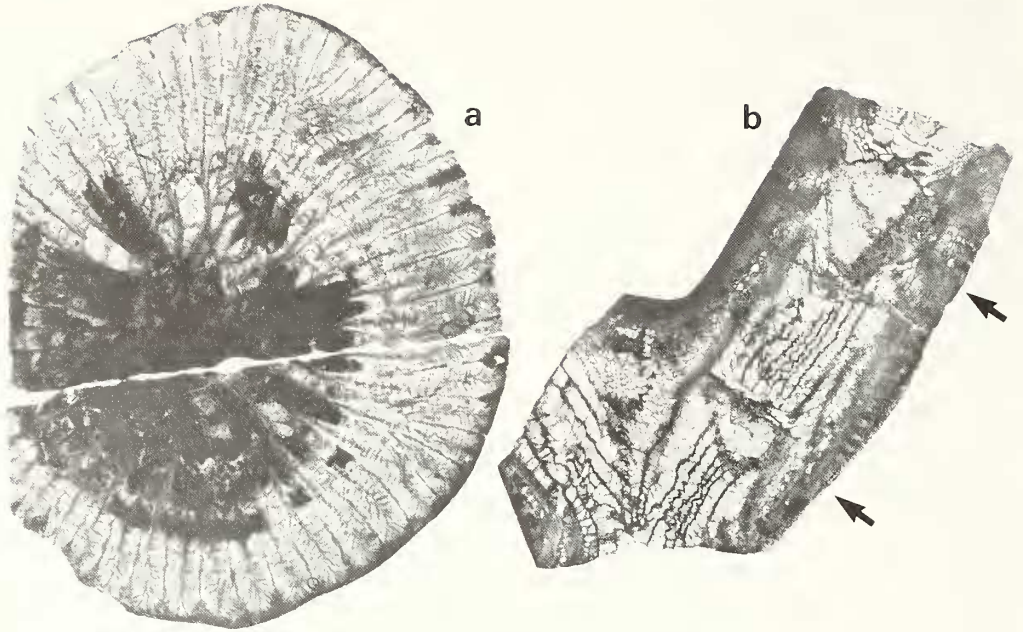
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#### EXPLANATION OF PLATE 92

Figs. 1-7. *Fromeophyllum climax* gen. et sp. nov. Mount Frome Limestone, near Mudgee, New South Wales. Early-Middle Devonian. 1-4, all from Unit D, 5-7 all from Unit A. 1, paratype USGD 21254b, transverse showing spoke-like septal ends,  $\times$  3. 2, paratype USGD 85234, transverse,  $\times$  3. 3, paratype USGD 21267, longitudinal of first- or second-order offset, showing dissepiments,  $\times$  9. 4, paratype USGD 21178, showing dissepiments and trabeculae,  $\times$  8. 5, paratype USGD 21176, transverse,  $\times$  3. 6, paratype USGD 85233, transverse through a massive and frequently budded portion of a colony,  $\times$  2. 7, paratype USGD 85233, longitudinal of different part of same colony as previous figure; specimen ruptured and zone of increase between trunk and offsets poorly preserved. Trabeculae, 'spongy' septa and characteristic dissepiments well preserved,  $\times$  4.



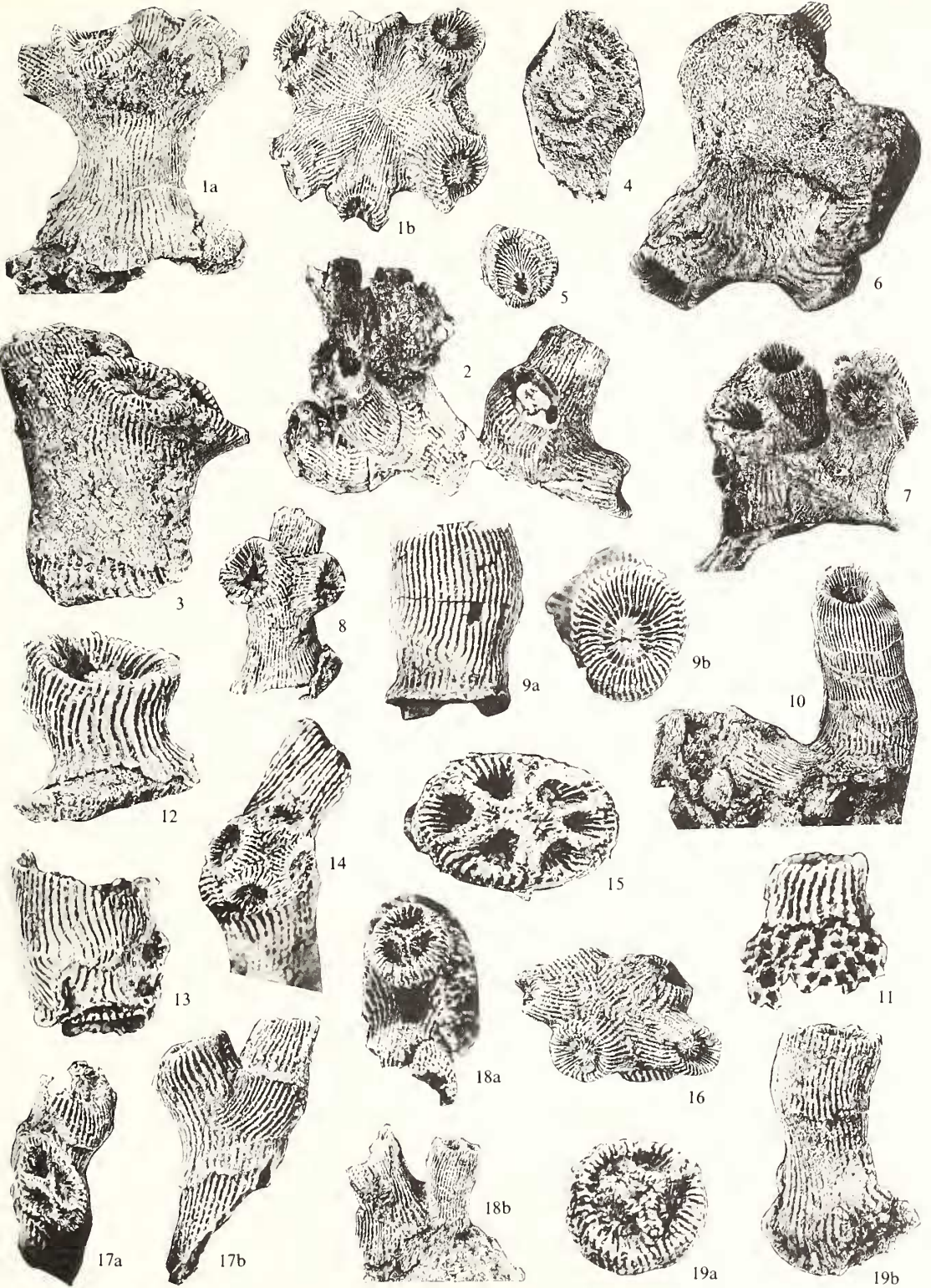
WRIGHT, *Fromeophyllum*



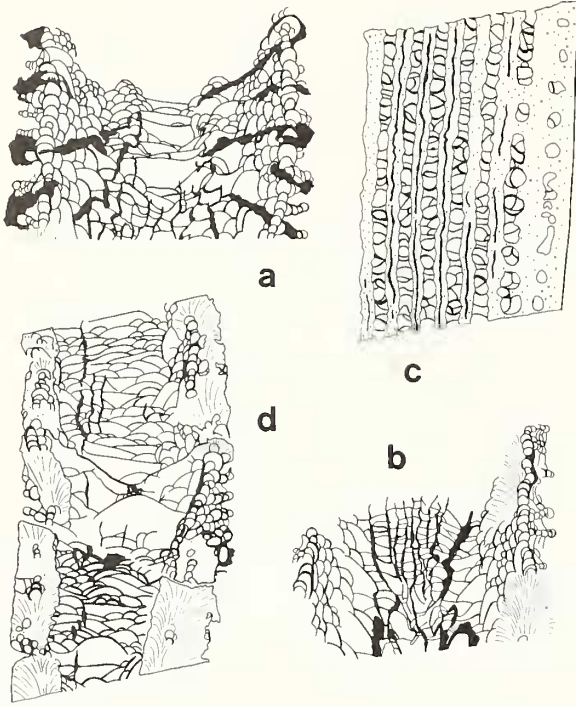
TEXT-FIG. 9. *Fromeophylloium climax*. *a*, paratype USGD 21175, transverse showing well-preserved trabeculae,  $\times 5$ . *b*, paratype USGD 21274, longitudinal of (probably) second-order offsets; the larger of the two shows two apparently aborted attempts at increase as indicated by spaces (arrows) in the tabularium,  $\times 3$ .

#### EXPLANATION OF PLATE 93

Figs. 1–19, *Fromeophylloium climax* gen. et sp. nov. Silicified specimens from Unit E, Mount Frome Limestone, near Mudgee, New South Wales, Early-Middle Devonian. 1*a, b* paratype USGD 85221, both  $\times 1$ . 1*a*, side view. 1*b*, dorsal view showing six first-order offsets. 2, paratype USGD 85222 showing three phases of increase,  $\times 1$ . 3, paratype AMF 60663, trunk showing discordant edge zone deposits secreted by first-order offsets,  $\times 1.5$ . 4, paratype USGD 85224, ventral view showing attachment surface with concentric growth increments,  $\times 1$ . 5, paratype AMF 60657, ventral view of juvenile trunk showing attachment surface,  $\times 1$ . 6, paratype AMF 60661, trunk specimen overgrowing a fragment of *F. climax*, and itself overgrown by tabulate coral material,  $\times 1$ . 7, paratype USGD 85225, lateral view of a probable composite colony,  $\times 1$ . 8, paratype AMF 60658, trunk showing three first-order offsets,  $\times 1$ . 9*a, b*, paratype USGD 88217. 9*a*, lateral view showing edge zone deposits,  $\times 1.5$ . 9*b*, calical view,  $\times 2$ . 10, paratype AMF 60659, lateral view of phototropic specimen with unusually constricted calyx,  $\times 1$ . 11, paratype USGD 85227, juvenile based on favositid coral,  $\times 3$ . 12, paratype USGD 85228, juvenile based on tabulate coral twig,  $\times 2$ . 13, paratype AMF 60665, lateral view showing edge zone deposits,  $\times 1.5$ . 14, paratype AMF 60664, four probable third-order offsets  $\times 1.5$ . 15, paratype USGD 85231, dorsal view showing six first-order offsets,  $\times 1.5$ . 16, paratype AMF 60656, dorsal view showing five first-order offsets,  $\times 1$ . 17*a, b*, paratype USGD 85230, both  $\times 1.5$ . 17*a*, calical view showing probable third-offsets. 17*b*, lateral view showing edge zone deposits, epitheca and abrupt contact (?overgrowth) between septa of two probable second-order offsets. 18*a, b*, paratype AMF 60660, a probable composite colony. 18*a*, dorsal view showing three diminutive first-order offsets,  $\times 1.5$ . 18*b*, side view,  $\times 1$ . 19*a, b*, paratype USGD 85229. 19*a*, calical view showing four juvenile first-order offsets,  $\times 2$ . 19*b*, lateral view showing trunk attached to tabulate twig,  $\times 1.5$ .



WRIGHT, *Fromeophyllum*



TEXT-FIG. 10. A, B, C longitudinal sections of *Fromeophyllum climax*. a, calical view, paratype USGD 85232,  $\times 3$ . b, calical view, paratype USGD 21273,  $\times 3$ . c, tangential section, paratype USGD 88220,  $\times 5$ . All from Unit D, Mount Frome Limestone, near Mudgee, New South Wales. Early Middle Devonian. d, *Macgeea touti* Pedder, paratype no. 6, UNE 8857 (Pedder 1966, pl. 6, fig. 8), longitudinal section. Sulcor Limestone, near Tamworth, New South Wales. Early Devonian.  $\times 3$ .

Innermost dissepiments globose or flattened, steeply inclined, and in two to four rows. Outside these six to ten horseshoes develop vertically in 2.5 mm; vertical continuity of series excellent, although individual horseshoes commonly asymmetrical. Outer zones of vertical, sometimes inosculating plates 0.5 to 1.0 mm in height, expand outwardly and up to 2 mm wide radially; plates less than 0.25 mm apart; height and length similar for alternating horizontal zones containing horseshoes. Both zones commonly contain plates more like globose dissepiments; also, for both zones, length and width may vary greatly within one corallite. Contact of horizontal zones with horseshoe series quite sharp but not necessarily rectangular. Outside these zones may be up to six rows of steeply outwardly inclined globose dissepiments; contact with horizontal zones almost always gradational and apparently produced by peripheral breakdown of horizontal zones. In view of the part horseshoe dissepiments normally played in acting as a base of trabecular fans, horseshoes in horizontal zones are quite exceptional in performing this function to only a very minor extent.

*Comparison.* The only species whose dissepimentarium closely compares with that of *F. climax* is *Macgeea touti* Pedder, 1966. The latter was described from calcareous specimens, from the Loomberah Limestone, and from the uppermost beds of the Sulcor Limestone, which occur near Tamworth, New South Wales; it is about 19 mm in diameter, has 18 to 24 major septa and compares well with first- and second-order offsets of *F. climax*. As noted by Pedder (1966), one of the *M. touti* paratypes (number 6, UNE 8857) has '... short subsidiary strings of horseshoe dissepiments (which) branch from the main collar into the outer part of the dissepimentarium'. Such a specimen seems close to the *F. climax* condition but it is not shared by all Sulcor specimens, some of which (e.g. paratype 5, UNE 8856) have a more normal *Macgeea*-like dissepimentarium. Paratype 8857 is refigured herein (text-fig. 10d). This material may preserve the transition from *Macgeea* to *Fromeophyllum*.

In gross external morphology and a general paucity of epitheca, *F. climax* can be compared with two Frasnian species—namely, *Pachyphyllum crassicoatum* Webster from Iowa (Webster 1889; Fenton and Fenton 1924) and *Pachyphyllum bouchardi* Milne-Edwards and Haime from Ferques (Lang and Smith 1935; Semenov-Tian-Chansky, Lafuste and Delga 1961). The latter species is known *inter alia* from a single topotype (Semenov-Tian-Chansky *et al.* 1961; Pl. 9, fig. 2) whose dissepimentarium is quite different from that of *F. climax*. *P. crassicoatum*, on the other hand, is relatively common, and seems to form larger colonies than *F. climax*, but internal structures have not been illustrated; overgrowth such as is described here from *F. climax* seems to be



present in a specimen illustrated by Fenton and Fenton (1924, pl. 9, fig. 1). My preference, especially in the case of *P. crassicostratum*, is to account for this similarity as a result of environmental control of growth form.

*Remarks.* The bizarre morphological feature of *F. climax*, the outer part of the dissepimentarium, is incompletely understood. The provisional interpretation of this feature is based on longitudinal sections located between septa, and tangential sections (e.g. text-fig. 10c). The variation seen in many sections results largely from the variation in the thickening of septa (in the region of the horizontal zones) with the attendant development of minor dissepiments. One of the alternating series of horizontal rows certainly contains mostly genuine horseshoes, above and below which are horizontal rows containing vertical plates. This is comparable to the relatively simple situation in *Macgeea* and *Thamnophyllum*, in which the dissepimentarium is dominated by a series of horseshoes flanked by flat plates. From this *Macgeea* condition it would be possible to generate the *Fromeophyllum* dissepimentarium by regular, repeated phases of calical extension. This would not, however, account for the outer normal part of the dissepimentarium nor the inclination of the trabeculae, which do not fan about the horizontal series of horseshoes. Further, the contact between the vertical and horizontal horseshoes is rectangular or nearly so, and not the smooth curve to be expected if the horizontal horseshoes had resulted from a natural lateral extension of the calyx. The regularity of this phenomenon must have a genetic basis.

*Thamnophyllum kozlowskii* (Rózkowska 1953) and *Thamnophyllum germanicum schoupeii* (Scrutton 1968) exhibit increase very similar to that of *F. climax*. There are many similarities in detail, including the formation of distally convex plates flooring the offsets and the continuity of some dissepimental and skeletal elements from the parent to the offsets (text-fig. 7a). *F. climax* is distinct in its paucity of epitheca and abundant and complex caenogenetic tissue (Soshkina 1953).

*Variation.* The external form (of silicified specimens) is extremely variable, and a high proportion of incomplete colonies occurs. The majority of incomplete colonies are trunks, which usually have some substrate still attached and have not undergone increase. They outnumber specimens which have undergone phase 1 increase by two to one. Many specimens have not survived past the early differentiation of first-order offsets. Although abundant 'branch' specimens occur, the number of colonies they represent is impossible to estimate. In some cases the substrate was brachiopod shell (Pl. 93, fig. 7) but the majority of aborted trunk specimens were attached to tabulate coral colonies or twigs (Pl. 93, fig. 19b) (many such specimens are strongly curved, especially basally where *F. climax* is wrapped around the twig). Instability of the twigs when the epifaunal load became excessive may have contributed to this mortality.

The height and diameter at which increase is initiated varies greatly (compare Pl. 93, fig. 1a with Pl. 93, figs. 18b, 19b), to the point where some diminutive first phases of increase closely resemble third phases in other specimens. Although deformed, many transverse sections across *F. climax* appear to have been originally slightly elliptical. Disregarding the expanded basal region and that increased diameter which commonly precedes increase, cross-sections of trunks vary up to about  $19 \times 12$  mm at which stage there are up to  $30 \times 2$  septa, although rarely there are up to  $38 \times 2$  septa. The rare specimens showing so many septa may show an unexplained and localized abundance of narrow septa; in specimens showing increase, this zone corresponds with one of the protofossulae which usually lie between offsets. Size alone is not a sufficient criterion to distinguish trunks from first- or rarely second-order offsets, as there are rare slender trunks (Pl. 93, fig. 19b) and, at the other extreme, offsets of relatively large diameters (Pl. 93, fig. 2). Septal counts and tabularium diameter are also of limited value in distinguishing some offsets from some trunks. Material from Units B and E is here assigned to *F. climax*. Some comment is necessary, especially in the case of Unit B from which only two branches and one substantial colony have been collected. Unit B material differs from material from Units D and E, as the septal dilation almost obscures the dissepimentarium (Pl. 92, figs. 5, 7). The above differences are here regarded as environmentally controlled.

The morphological variation in growth form seen in *F. climax* may be closely paralleled by certain Late Devonian tetracorals from the Ferques area in the Boulonnais. In particular, *Macgeea gallica*

Lang and Smith is reputed to be solitary or feebly colonial, and 'can hardly be separated from' the phaceloid *Pachyphyllum bouchardi* Milne-Edwards and Haime (Smith 1945, p. 38). Broken calcareous colonies of *Fromeophyllum* often give the impression of coexisting solitary and colonial forms. According to Smith (1945) *Macgeea* includes solitary and weakly colonial forms.

*Preservation.* Throughout most of its stratigraphical range, *F. climax* is preserved as calcareous specimens embedded in limestone and rarely as material weathering out of poorly exposed marls. Silicified material is restricted to a horizon up to 1 m thick at the very top of the range of the species (Unit E, 139.9 m). Calcareous material provides the information about internal morphology. Almost all information about external morphology is derived from silicified specimens which are more properly described as having only a silicified skin. The depth and quality of silicification is such that treatment with an acetone-soluble impregnating agent is essential; this has led to permanent attachment of debris to some specimens. The fragility of silicified material is further aggravated by the pervasive tectonic deformation which has affected these rocks so that in some specimens the original shape (and dimensions) are rather conjectural.

*Palaeoecology.* While calcareous specimens of *F. climax* give clear indication in many longitudinal and transverse sections of an edge zone, silicified specimens from Unit E provide considerable information about the preference of *F. climax* for certain types of substrate. There is, in available material, a high incidence of attachment of *F. climax* to hard objects by its expanded basal region. The most common substrate favoured by planulae was the shell of *Megastrophia* sp. (a stropheodontid brachiopod), especially the convex exterior of large pedicle valves. Less common as a substrate are stick-like tabulate corals (Pl. 93, fig. 19b) and fragments of *F. climax* itself (Pl. 93, fig. 6). Rarely, favositid colonies have epifaunas including *F. climax*, algae, and auloporid tabulate corals (Pl. 93, fig. 13). There must have been considerable competition for a firm substrate elevated above the silty floor, and in many cases *F. climax* individuals have overgrowths of algae, tabulate corals, or stromatoporoids, which might sometimes have caused the death of the *Fromeophyllum*.

The extent of the edge zone is poorly known in most growth stages, as epitheca is absent or perhaps only preserved as remnants. Certainly colony trunks, prior to phase 1 increase, may have undergone several phases of 'overflow' of skeletal material down to the substrate. Offsets, certainly first-order offsets, and presumably second- and third-order offsets, mostly had a functional edge zone. The proximal extent of soft parts down the exterior of the uninhabited branch below the calyx is uncertain so offsets may or may not have had connecting soft parts. Examination of proximal regions of morphologically similar tetracoral colonies may show that this edge zone was widely developed, being necessary for the purposes of stability.

## CONCLUSION

Although far from ideal preservation, this Mount Frome material permits the rare and informative opportunity to study complex external and internal morphology and their interrelationship. *F. climax* had a functional edge zone, a feature considered by Wells (1957) to be developed in Palaeozoic corals to a very limited extent and then mostly in the form of talons or rootlets. If the development of an edge zone in post-Palaeozoic corals was such an important advantage (Wells 1957) then the failure of *F. climax* to found a dynasty must be attributed to either the obliteration of the appropriate marine environment in this part of New South Wales or some inappropriate aspect of this morphological venture at this time and place.

The function of the horizontal rows of dissepiments remains obscure and unexplained.

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A. J. WRIGHT

Department of Geology  
University of Wollongong  
P.O. Box 1144, Wollongong, N.S.W. 2500  
Australia

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